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Michenia, a New Protolabine (Mammalia, Camelidae) and a Brief Review of the Early Taxonomic History of the Genus *Protolabis*

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INTRODUCTION

In 1876 E. D. Cope erected the monotypic genus *Protolabis* on the basis of *Procamelus heterodontus* Cope, 1873. Unlike *Procamelus,* in which the first upper incisor is lost, the type specimen of *Protolabis heterodontus* retains a full set of upper incisors. The type of *Protolabis heterodontus* consists of a worn upper dentition and a partial left ramus that were poorly understood by subsequent authors who continued to refer their species to *Procamelus* rather than to *Protolabis.* This confusion was further compounded by the fact that four species that are here recognized as belonging to *Miolabis* were incorrectly referred to *Protolabis.*

In order to clarify the taxonomic status of *Protolabis,* a brief critical review of the literature is given along with characters that distinguish *Protolabis* from *Procamelus* and *Miolabis.* A new protolabine genus and species are also described.

The late Childs Frick was the first to recognize the new taxon described in the present report. Several of the figures were prepared under his

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direction, and his manuscript and notes were utilized in writing the final version of the text. The manuscript and notes represent only a part of Frick's extensive revision of the Camelidae. The junior author worked closely with him during the many years of his study of the Camelidae. Because Frick's work was unfinished, the junior author provided the final version of the text and is responsible for its revised contents.

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The following abbreviations are used:

A.M.N.H., the American Museum of Natural History
C.I.T., California Institute of Technology
C.M., Carnegie Museum
F:A.M., Frick American Mammals, the American Museum of Natural History
P.U., Princeton University Museum

PROTOLABIS COPE

Historical Résumé

Procamelus heterodontus from northeastern Colorado was named and partially diagnosed by Cope at a meeting of the Academy of Natural Sciences in Philadelphia on December 23, 1873. The name was subsequently published in the Proceedings of the Academy (1873, p. 420), but this publication was not issued until February 17, 1874. Meanwhile a more complete description with measurements of the type of *Procamelus heterodontus* was given by Cope (1874, p. 20), along with the description of another new camelid species, *Procamelus angustidens,* also from northeastern Colorado. Ironically, Cope's description of *P. angustidens* was placed ahead of *P. heterodontus* on page 20, and this report was published a month earlier (January, 1874) than the date of issue for the 1873 Proceedings which was in February, 1874.

In 1874 Cope found an almost complete skull and partial skeleton, that is now recognized to be *Protolabis,* in the "Santa Fe marls" of New

Mexico. Cope (1877, p. 329) referred this partial skeleton to *Procamelus occidentalis* Leidy, 1858a. He observed that the skull of this not fully mature individual had an alveolus on one side that contained the crown of a small second incisor, but on the opposite side the corresponding alveolus was shallow and empty. Because the last molar was not fully erupted, Cope surmised that the incisor was temporary and shed before maturity. In contrast, the premaxilla of the type of *Procamelus heterodontus* has a large I^3 and moderately large alveoli for I^{1-2}, with an additional alveolus for a deciduous incisor. Cope realized that in allocating the Colorado species to *Procamelus* he had ascribed wrongly a full complement of upper incisors to *Procamelus,* and he therefore proposed a new genus, *Protolabis* (1876, pp. 144–145), which was diagnosed as having a full set of upper incisors.

Matthew (1901, p. 434) transferred Cope's *Procamelus angustidens* Cope, 1874 to *Protolabis* and stated (p. 433), "As the nomenclature now stands this [*Protolabis heterodontus* Cope] is the type species of the genus; but should further material prove it impossible to maintain the distinction between it and the previously described *Procamelus angustidens,* it will become a synonym of that species, which then becomes the type of the genus. The only distinction in the type specimens is the position and character of the first premolar of the lower jaw, which in *P. heterodontus* is further forward and subcaniniform." Webb (1969, p. 148) listed *Protolabis angustidens* as a synonym of *P. heterodontus.* This is substantiated by additional specimens in the Frick Collection from the type area which show considerable variation in the position of the P_1 and the length of the diastema. Although *Procamelus angustidens* Cope (1874, p. 20) has page precedence over *Procamelus heterodontus,* Matthew's statement concerning the synonymy of *Protolabis heterodontus* with *Protolabis angustidens* is not here considered applicable. When Cope proposed the new genus *Protolabis* in 1876 he stated, "The typical and only known species is *Protolabis heterodontus,* Cope, from the Loup Fork beds on Northeast Colorado." *Protolabis heterodontus* is therefore the type species (type by original designation) in accordance with Article 68a in the International Code (Stoll and others, 1961).

In 1879 Cope described *Protolabis transmontanus* from the Mascall Formation in Oregon. Cope assigned *transmontanus* to *Protolabis* because of the large upper incisors in the type (A.M.N.H. No. 8196), but he also pointed out numerous ways in which *P. transmontanus* differed from *P. heterodontus.* Wortman (1898, pp. 122–123) restricted *Protolabis* to *P. transmontanus,* and placed *Protolabis heterodontus* Cope, 1873 (genotypic species) and *Protolabis prehensilis* Cope, 1881 in synonymy with *Procamelus robustus* Leidy, 1858b.

Hay (1899, p. 593) accepted Wortman's transfer of the genotypic species, *P. heterodontus* to *Procamelus,* proposed a new genus, *Miolabis,* and selected the Mascall species, *transmontanus,* as the type of *Miolabis.* Even after *Miolabis* was described, species of this genus continued to be referred to *Protolabis.*

Four species formerly and incorrectly placed with *Protolabis* are here recognized as belonging to *Miolabis.* These are: (1) *Procamelus fissidens* Cope, 1876, type (A.M.N.H. No. 8297); (2) *Protolabis montanus* Douglass, 1899, type (C.M. No. 702); (3) the skull, jaws, and partial skeleton (A.M.N.H. No. 9108) from Cedar Creek, Colorado, referred by Matthew (1901, p. 435) to *Protolabis montanus* and later selected by Matthew (1909, p. 115) as the type of *Protolabis longiceps;* and (4) *Protolabis princetonianus* Sinclair (1915, p. 87), type (P.U. No. 12053). A taxonomic history of these species is given in the present paper in greater detail. Cope (1874, p. 22) referred a partial mandible from Pawnee Creek, Colorado, to *Procamelus occidentalis* Leidy. Two years later Cope (1876, p. 145) selected this partial mandible as the type of a new species, *Procamelus fissidens,* which Matthew (1924, p. 190) subsequently transferred to *Protolabis.* Douglass (1899, p. 13) described new material from Montana as *Protolabis montanus.* Sinclair (1915, p. 87) selected a skull and mandible from the Lower Snake Creek deposits of Sioux County, Nebraska, as the type of *Protolabis princetonianus,* whereas Matthew (1924, p. 190) listed the latter as a synonym of *Protolabis fissidens* Cope of Colorado.

Matthew (1901, p. 435) referred and figured a skull, jaws, and partial skeleton (A.M.N.H. No. 9108) of *Miolabis* from Cedar Creek, Colorado, to *Protolabis montanus* Douglass. Matthew's figures of the limbs of this incorrectly referred specimen[1] (A.M.N.H. No. 9108) are responsible for the widespread and erroneous concept that the metacarpals and metatarsals are completely unfused in the genus *Protolabis.*

Metapodials are completely fused in *Protolabis,* and this was shown in the first illustration of a *Protolabis* metapodial published by Cope (1877, pl. 79, figs. 6, 6a) under the name *Procamelus occidentalis* Leidy. This specimen from the "Santa Fe marls" of New Mexico, described by Cope (1877, p. 329) consisted of a skull, jaws, and partial skeleton, including the solidly fused metacarpus. The skull, jaws, and limbs are nearly duplicated by *Protolabis* remains in the Frick Collection from New Mexico. This assignment is further verified by associated skeletal remains of *Protolabis* with fused metapodials from Nebraska and California.

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[1] Later, this same specimen was selected by Matthew as the type of *Protolabis longiceps* Matthew, 1909 = *Miolabis longiceps* (Matthew, 1909).

A review of the literature shows that *Protolabis* species have frequently been mistaken for *Procamelus* species, although they are readily distinguishable in many ways. The main features by which *Procamelus* can be separated from *Protolabis* are as follows: the dentition of *Procamelus* is larger than that of *Protolabis,* it has lost I^1 and in most species I^2 is also lost, and the molars are more anteroposterioly expanded and taller-crowned. The metapodials of *Procamelus* are proportionally heavier with the length of the metacarpus exceeding that of the metatarsus, whereas in *Protolabis* the length of the metacarpus is always less than that of the metatarsus.

The historical record also shows that species of *Miolabis* have often been confused with those of *Protolabis. Miolabis* is distinguished from *Protolabis* by the (1) larger and conspicuously cupped I^{1-2}, (2) absence of P_1, (3) relatively stouter and less laterally compressed premolars, (4) lower-crowned molars with stronger metastylids, (5) less anteroposteriorly expanded M_3^3, and (6) proportionally shorter, unfused metapodials.

SYSTEMATICS

CLASS MAMMALIA LINNAEUS, 1758

ORDER ARTIODACTYLA OWEN, 1848

SUBORDER TYLOPODA ILLIGER, 1811

FAMILY CAMELIDAE GRAY, 1821

SUBFAMILY CAMELINAE GRAY, 1821

TRIBE PROTOLABIDINI ZITTEL, 1893

INCLUDED GENERA: *Protolabis* Cope, 1876; and *Michenia,* new genus.

MICHENIA, NEW GENUS

TYPE: *Michenia agatensis,* new species.

DISTRIBUTION: From early Hemingfordian (medial Miocene of North America) to late Clarendonian (medial Pliocene of North America) in the western United States.

INCLUDED SPECIES: Type only.

DIAGNOSIS: *Michenia* differs from *Protolabis* by its smaller size; much narrower muzzle; weaker and more incisiform I^{1-3} and upper canine; P^{2-3}_{2-3} relatively larger and less laterally compressed with more distinct cusps; lower-crowned molars with stronger vertical ribs on the paracone and metacone and more prominent metastylids; less anteroposteriorly expanded M_3^3; shallower symphysis, which is conspicuously unlike the deep and more ventrally produced symphysis in *Protolabis*; shallower

TABLE 1

SUMMARY OF DIAGNOSTIC CHARACTERS THAT DISTINGUISH *Michenia agatensis*, NEW GENUS, NEW SPECIES, FROM *Protolabis heterodontus* (COPE), GENOTYPIC SPECIES

	Michenia agatensis	*Protolabis heterodontus*
Length of M_3	28.5 to 29 mm.	38 to 47 mm.
Muzzle	Extremely narrow	Moderately wide
I^{1-3} and C	Weak and incisiform	I^{1-2} reduced; I^3 and C caniniform, larger. Vary from medium size in female, to large in male
Lower canine	Semi-incisiform, somewhat laterally compressed, and closely grouped with incisors	More caniniform, slightly less anteriorly placed
Premolars	Moderately larger, with distinct cusps on P^{2-3}_{2-3}	Relatively smaller, simpler, more laterally compressed, with less distinct cusps on P^{2-3}_{2-3}
Molars	Lower-crowned with strong vertical ribs on paracones and metacones; strong metastylids	Taller-crowned. Weak vertical ribs on paracones and metacones; weak metastylids
M^3_3 anteroposterior expansion	Unexpanded	More expanded, longer relative to first molar; hypoconulid relatively longer
Symphysis	Shallow	Deeper: noticeably deeper, with posterior part of symphysis projected more ventrally
Horizontal ramus	Shallow	Deep
Metapodials	Elongate, slender, less solidly fused; metacarpals and metatarsals III and IV have deeper groove along line of fusion	Shorter, heavier, more solidly fused
Length of metacarpus relative to length of skull	Greater than basal length of skull	Less than basal length of skull
Length of metacarpus relative to length of metatarsus	Slightly longer than metatarsus	Shorter than metatarsus

horizontal ramus; and proportionally longer and slenderer metapodials. In *Michenia* the metapodials are less solidly fused than in *Protolabis* and both metacarpus and metatarsus have a deeper groove along the line of fusion. Moreover, the anterodistal separation of the distal ends of both the metacarpus and the metatarsus extends proximally farther up the shaft in *Michenia* than in *Protolabis*. The length of the metacarpus in *Michenia* exceeds the basal length of the skull and is slightly longer than

the metatarsus. This difference in length is reversed in *Protolabis,* with the length of the metacarpus less than either the basal length of the skull or the length of the metatarsus.

DISCUSSION: *Michenia* is based on rare and heretofore unpublished remains that were collected by the American Museum Expedition of 1908, from the Upper Harrison beds[1] of Peterson, 1906 (=the Marsland Formation of Schultz, 1938), 5 to 6 miles northeast of the former post office of Agate, Nebraska. This is the earliest known protolabine occurrence. Even at this early stage of development, *Michenia* exhibits the general protolabine characters that include (1) a tendency toward size reduction of the premolars in comparison to the molars, (2) reduction in size of I^{1-2}, (3) moderately tall-crowned molars with weak metastylids, and (4) nearly solidly fused metapodials.

The type of *M. agatensis* (A.M.N.H. No. 14255) and A.M.N.H. Nos. 14259 and 14261 were referred to *Oxydactylus lulli* Loomis by Matthew in his unpublished manuscript on the revision of the Camelidae. Matthew pointed out numerous ways in which the Agate specimens differed from *O. lulli* including: smaller size, the elongate slender muzzle, smaller caniniform teeth, more hypsodont molars, and more co-ossified metapodials. In addition, a comparison with *Oxydactylus* dentitions shows that the premolars were relatively smaller and more laterally compressed, whereas the molars are not only taller-crowned but tend to have weaker mesostyles and less prominent metastylids.

In 1935 Stock described *Dyseotylopus migrans* from the upper part of the Sespe Formation of California. He discussed the relationship of *Dyseotylopus*[2] with other known genera and concluded that it was "an advanced poebrothere" and stated, "Possibly *Dyseotylopus* and *Protomeryx* are congeneric." The type of *D. migrans,* a partial skull (C.I.T. No. 1721), has a broad maxillary fossa that is similar to that found in the type of *M. agatensis.* In the type of *D. migrans,* P^4 is of moderate size, and is proportionally about the same size relative to M^3 as it is in *M. agatensis.* P^2 and P^3 are broken in the type of *D. migrans,* but the roots indicate that they were relatively smaller than in *Oxydactylus,* and are more nearly comparable in size to those of *M. agatensis.* The molars in *D. migrans* were described by Stock (1935, p. 121) as being "compressed transversely and higher crowned than in *Poebrotherium* or *Paratylopus.*" Although the molars

[1] The Upper Harrison beds are here presumed to be equal to the "Lower Marsland" as interpreted by McKenna in a footnote (1965, p. 14).

[2] McKenna (1968, p. 4) stated, "It is possible . . . that Stock's *Dyseotylopus* . . . is a junior synonym of *Miotylopus* . . ."

in *D. migrans* are taller-crowned than other Arikareean camelids except the stenomylines, they are lower-crowned than in *M. agatensis.* The mesostyles are weak in *D. migrans* and, as observed by Stock, do not extend the full length of the crown. In *M. agatensis* the mesostyles are comparatively weak but stronger than in *D. migrans* and less prominent than in *Oxydactylus.*

Unfortunately the limbs of *D. migrans* are as yet unknown, but if the metapodials are found and prove to be elongate and partially co-ossified, they would be basically similar to those of *Michenia.* Despite the fundamental differences in the dentition, *Michenia agatensis* more closely resembles *Dyseotylopus migrans* than any other known Arikareean camelid.

Undescribed remains of *Michenia* are recognized in deposits from early Hemingfordian to late Clarendonian age. *Michenia* has a wide geographical range extending from California east to Texas, and north to Wyoming. The present paper is only an interim report on the protolabines; a complete study of the group will be published later. Until additional species are described, the characters of the genus are those of the type species, *Michenia agatensis.*

Michenia agatensis, new species

Figures 1–4

TYPE: A.M.N.H. No. 14255, partial skull and mandible with I_1^1–M_3^3, both partial humeri, right radius and left partial radius, right scaphoid and lunar, distal end of metacarpus, two complete and one broken first phalanges of the manus, left femur, left tibia and separate malleolar bone, left astragalus and calcaneum, left metatarsus and one broken rear first phalanx, and three broken cervicals. The type is from the Upper Harrison beds of Peterson, 1906 (=the Marsland Formation of Schultz, 1938), 6 miles northeast of the former post office of Agate, Sioux County, Nebraska.

DISTRIBUTION: From the Upper Harrison beds of Peterson, 1906 (=the Marsland Formation of Schultz, 1938), Sioux County, Nebraska.

HYPODIGM: From the type locality 5 to 6 miles northeast of Agate, Sioux County, Nebraska: type and A.M.N.H. No. 14259, partial skeleton including detached P^4–M^3, mandible with I_1(br.)–M_3, partial scapula, right humerus, both ulnoradii, both metacarpi, both unciforms, partial pelvis, right femur, patella, right articulated tibia, malleolar, astragalus, and calcaneum, left astragalus, right articulated cuboid, ectocuneiform and metatarsus, six first phalanges, four second phalanges, one third phalanx, and vertebrae, from 5 miles northeast of the former post office of Agate; A.M.N.H. No. 14261, posterior half of skull with P^3–M^3, atlas, axis,

humeri, radii, metacarpi, carpals, phalanges, and a block of vertebrae and ribs; A.M.N.H. No. 14256, distal part of humerus, carpals, including cuneiform, lunar, unciform and magnum, proximal part of metacarpus, partial femur, and partial tibia, from 6 miles northeast of the former post office of Agate.

DIAGNOSIS: Only known species of the genus.

MEASUREMENTS: See tables 2 and 3.

DESCRIPTION

SKULL: Two partial skulls of *Michenia agatensis* were recovered from the type locality, 5 to 6 miles northeast of Agate, Sioux County, Nebraska. The type skull (A.M.N.H. No. 14255) is dorsoventrally crushed and the nasals and maxillae are incomplete. Despite some crushing, the over-all cranial characters are apparent and can be compared with those of *Protolabis.* Primarily, the skull of *Michenia agatensis* differs from that of *Protolabis heterodontus* in its smaller size, narrower muzzle, weaker incisors and canine, proportionally larger premolars, and smaller molars.

In the type of *Michenia agatensis* the basal length of the skull (A.M.N.H. No. 14255) is 237 mm. and the P^2–M^3 length is 100.8 mm. When these measurements are compared with those of the type[1] of *Protolabis heterodontus* (A.M.N.H. No. 8296) and those of a referred partial skull[2] (A.M.N.H. No. 9426), both from the Pawnee Creek area of Colorado, the tooth row is approximately 25 per cent longer than in *Michenia agatensis* and the basal length is estimated to be even more than 25 per cent longer. Anterior to P^2, the muzzle is extremely narrow and delicate, with the width of the muzzle remaining almost constant and not noticeably wider around I^3 and the upper canine, as in *Protolabis heterodontus.*

Unfortunately, the nasal processes of the premaxilla and the anterior part of both the nasals and the maxilla are missing. The maxillary bone is high above the cheek teeth and marked by a large, moderately deep fossa. Although the maxillary bone is broken away near the forward border of the fossa, the anteroposterior diameter of the fossa is estimated to be 37 mm. The fossa is more oval than round, with the anterior part above P^2 and the posterior border above M^1. A small infraorbital foramen is situated beneath the maxillary fossa and above the posterior part of

[1] The only available data for the type (A.M.N.H. No. 8296) is "Pawnee Creek beds, near Pawnee Buttes, Weld Co., Colorado" (*fide* Cope and Matthew, 1915).

[2] The referred skull (A.M.N.H. No. 9426) was collected by Barnum Brown in 1901 from 40 feet above the base of the lower part of the Pawnee Creek Formation (excluding equivalents of the Martin Canyon beds of Matthew, 1901), 3 miles east of Pawnee Buttes, Colorado.

P^4. Anterior to the orbit is an extremely large lacrimal vacuity, which is bordered by the lacrimal, frontal, nasal, and maxillary bones. The anterior border of the vacuity is separated from the maxillary fossa by a narrow bridge (7 mm. at the narrowest point). Compared with the large vacuity, the lacrimal bone is relatively small, for anteroposteriorly it measures only 6 mm. at the narrowest point. The interorbital region of the frontal is only moderately wide with a slight median depression. Situated between the orbital rim and the median frontal suture, but nearer to the suture, is a very small supraorbital foramen.

Compared with the size of the skull, the orbits are large. Although the supraorbital process is broken in the type, the zygomatic process of the malar extends upward and presumably would have closed the orbit posteriorly. Bordering the front and lower half of the orbit, is a relatively light malar bone that has a slightly concave rugose surface for the attachment of the anterior masseter muscle. Leading forward from the malar for a short distance onto the maxilla, is a moderately strong masseteric ridge. In the type of *Michenia agatensis,* the zygomatic process of the malar is light and extends posteriorly and upward to about midorbit. The zygomatic process of the squamosal is even lighter than that of the malar and extends forward to join the latter just posterior to the orbit.

Compared with the length of the skull, the cranium is short, but elongation of the muzzle in the type is partly responsible for this over-all proportion. The parietal and supraoccipital regions are eroded, so that most sutures are obscure. In the type, extremely weak frontoparietal ridges run posteriorly from the posterior border of the orbit. About 20 mm. behind the frontoparietal suture, the parietal ridges join; the parietal and supraoccipital regions posterior to this junction are so damaged that the presence of a weak sagittal crest can be only surmised. A moderately strong sagittal crest is present, however, in a referred partial skull (A.M.N.H. No. 14261). In *Michenia* the occiput is low. A prominent temporal crest extends posteriorly to join the prominent lambdoidal crests. Viewed from the rear, the occiput is narrow and tends to be small relative to the size of the skull. In the type (A.M.N.H. No. 14255), the occipital bones are fused, and the sutures, for the most part, are obscure. The occipital condyles are situated anterior to the plane of the occiput and the basicranial axis is moderately flexed.

In a referred partial skull (A.M.N.H. No. 14261) the auditory bulla is moderately inflated and conforms to the general camelid pattern. The bulla, however, tends to be less laterally compressed than in later occurring species of *Protolabis* and is marked by a deep hyoidal pit in A.M. N.H. No. 14261, with the tip of the hyoid still in place. The external

auditory meatus is an almost cylindrical, closed ring, in which the anterior border forms a weak projecting lip. The paroccipital process is directed ventrally and slightly anteromesially and is fused with the bulla for most of its length; it extends ventrally to the level of the bulla. In *Michenia* the transverse diameter of the glenoid fossa is relatively wide as in *Protolabis,* but the anteroposterior diameter is less. Such a fossa would permit less fore-and-aft movement of the mandible in *Michenia.* Closely appressed to the bulla is a low, almost vertical postglenoid process, and directly behind that, with its anterior wall confluent with the process, is an extremely large, cylindrical postglenoid foramen. In *Michenia* (A.M.N.H. No. 14261) the postglenoid foramen is as large as the external auditory meatus and larger than in *Protolabis.* The posterior nares open between the palatines just behind the posterior loph of M^3. In *Michenia agatensis* the anterior border of the narial opening is about parallel to the third molars, whereas in *Protolabis heterodontus* the narial opening is slightly more posterior. Although the palatal surface is broken away in the type, enough is left to show that the palate is only slightly depressed between the molars but is deeply concave in the premolar region. The palatine process of the maxilla is moderately wide between the molars as in *P. heterodontus* but anteriorly narrower than in the latter. In the type of *M. agatensis* the muzzle is extremely narrow between P^1 and P^2 and the broken palatine process of the premaxilla is delicate.

Upper Dentition: I^3, C, P^4, M^3. The upper incisors, canine, and anterior premolars are present only in the type of *M. agatensis* (A.M.N.H. No. 14255). *Michenia agatensis* stands apart from contemporary camelids and already exhibits protolabine characters including: (1) a reduction in size of I^{1-2}, (2) a tendency toward the reduction in size of the premolars, and (3) taller-crowned molars with weak metastylids.

The most striking feature of the rostrum is the presence of small, uncrowded incisiform teeth. I^1 and I^2 are nearly identical; both incisors are laterally compressed with the crowns of each curving mesially. The lateral surface of each incisor is convex and the mesial surface is concave. A short space (2.5 mm.) separates I^1 from I^2; I^3 is similar in form to I^1 and I^2, but is slightly larger, less compressed laterally, thicker transversely, with a less concave mesial surface. A longer diastema (6.5 mm.) separates I^2 from I^3 than from I^1. The upper canine closely resembles I^3, but it is slightly larger and separated from the canine by a diastema measuring 11.5 mm. Both I^3 and the canine are heavier, less mesially curved, and more caniniform than the first two incisors. In *Protolabis heterodontus,* I^3 and C are strongly caniniform and relatively larger than in *Michenia agatensis.* Between the canine and the first premolar in *M.*

TABLE 2

WEAR AND MEASUREMENTS (IN MILLIMETERS) OF LENGTH AND WIDTH OF UPPER AND LOWER TEETH AND DIASTEMATA OF *Michenia agatensis*, NEW SPECIES, AND *Protolabis heterodontus* (COPE)

	A.M.N.H. No. 14255[a]	A.M.N.H. No. 14259	A.M.N.H. No. 14261	A.M.N.H. No. 8296[b]	A.M.N.H. No. 8294	A.M.N.H. No. 9426
Wear[c]	W2	W2	W3	W3	W3	W2
Upper dentition						
I^1	4.0 × 2.3	—	—	—	—	—
I^2	4.0 × 2.5	—	—	—	—	—
I^3	4.5 × 3.0	—	—	10.4 × 8.4	—	—
I^3–C/ diastema	11.5	—	—	7.8	—	—
C/	4.8 × 3.0	—	—	11.5 × 8.5	—	—
C/–P^1 diastema	16.0	—	—	15.5	—	—
P^1	6.0 × 3.8	—	—	9.5 × 5.2	—	—
P^1–P^2 diastema	17.1	—	—	—	—	—
P^2	11.4 × 4.5	—	—	—	—	—
P^3	12.9 × 7.5	—	br.	—	—	(17)[d] × —
P^4	12.6 × 9.9	12.5 × 10.0	15.0 × 10.8	(15) × 14.6	—	18.0 × 12.8
M^1	18.0 × 16.0	18.0 × 16.9	(17) × 17.0	(21.2 +) × (20.2)	—	(24.5) × —
M^2	24.0 × 18.0	22.9 × (16)	25.5 × 19.5	32.0 × 25.0	—	(35) × (25)
M^3	23.9 × 16.0	23.0 × (15)	27.8 × 19.5	35.2 × 22.5	—	39.8 × 23.0
P^2–M^3	93.0	—	—	—	—	(127)
Lower dentition						
I_1	8.5 × —	br.	—	—	—	?

TABLE 2—(*Continued*)

	A.M.N.H. No. 14255[a]	A.M.N.H. No. 14259	A.M.N.H. No. 14261	A.M.N.H. No. 8296[b]	A.M.N.H. No. 8294	A.M.N.H. No. 9426
I_2	11.0 × —	9.1 × –	—	—	14.6 × —	12.8 × —
I_3	10.0 × —	10.7 × –	—	12.5 ×	19.5 × —	16.5 × —
/C	6.5 × 4.0	6.0 × 3.5	—	12.0 × 8.3	9.6 × 7.5	8.5 × 7.0
/C–P_1 diastema	16.8	11.0	—	13.5	20.0	21.0
P_1	6.3 × —	9.0 × 3.7	—	10.6 × 4.8	9.0 × 4.1	9.5 × 3.9
P_1–P_2 diastema	20.6	19.0	—	37.0	22.2	27.8
P_2	9.9 × 4.0	8.5 × 3.7	—	9.7 × (4.5)	11.0 × 4.1	9.8 × 3.4
P_3	11.5 × 4.5	10.5 × 4.4	—	12.7 × br.	12.5 × 5.0	11.8 × 4.8
P_4	13.9 × 6.6	12.5 × 6.1	—	—	16.0 × 7.5	16.5 × 8.0
M_1	16.0 × 10.3	16.6 × 11.0	—	—	(19 +) × (14 +)	(21.7 +) × 13.4
M_2	23.5 × 12.0	22.0 × 12.7	—	—	32.2 × 19.0	33.0 × 17.5
M_3	29.0 × 12.0	28.5 × 12.0	—	—	47.5 × 18.0	47.0 × 16.0
P_2–M_3	100.8	96.0	—	—	134.8	133.5

[a] A.M.N.H. No. 14255 is the type of *Michenia agatensis,* new species. A.M.N.H. Nos. 14259 and 14261 are referred.

[b] A.M.N.H. No. 8296 is the type of *Protolabis heterodontus* Cope. A.M.N.H. No. 8294, the type of *Protolabis angustidens* (Cope), and A.M.N.H. No. 9426 are referred to *Protolabis heterodontus.*

[c] Wear terminology modified after Skinner (1942, p. 189); W, premolars starting to wear, first molar retains anterior fossette; W1, anterior fossette of first molar worn away and posterior fossette wearing smaller. Articulated skull and mandibles show that the superior dentition wear count is different by one or more stages less than the inferior. For example in the type (A.M.N.H. No. 14255) the anterior fossette of the first upper molar is not yet quite worn away but the posterior fossette of the first lower molar has already disappeared.

[d] Measurements enclosed in parentheses are approximate.

agatensis is a moderately long diastema (16 mm.). P^1 is small, double-rooted, simple-crowned, with the paracone rising to a blunt peak. A long diastema (17.1 mm.) separates P^1 from P^2. Each diastema separating these rostral teeth from I^1 back becomes progressively longer. P^2 is elongate, bladelike, double-rooted, and relatively longer and more complex than that of *P. heterodontus.* P^2 has a small parastyle and a high main cusp that is in the position of the paracone. Posterior to this central cusp (paracone), the tooth tends to be divided between what would seemingly correspond to the metacone and a small metastyle. No protocone is present but a weak lingual cingulum foreshadows the stronger cingulum and weak protocone on P^3. P^2 in *M. agatensis* is relatively larger with more distinct cusps than the simpler, laterally compressed, bladelike P^2 in *P. heterodontus.* P^3 is also a narrow, elongate tooth that is similar to P^2 except for its larger size, stronger lingual cingulum, and an incipient protocone. P^4 is single-lobed with inner and outer cusps separated by a deep fossette. Anteroposteriorly, P^4 in *M. agatensis* is about the same length as P^3 but the enlarged protocone gives P^4 a much greater transverse diameter. P^4 is characterized by a high paracone, a strong parastyle, an incipient metastyle, and a large protocone. Except for the parastyle, the buccal surface of P^4 is almost smooth with only a faint trace of a vertical rib on the paracone.

The upper molars of *M. agatensis* are smaller (table 2) and lower-crowned than those of *P. heterodontus;* otherwise, the molars are similar in cusp morphology. Each molar is bilobed with deep fossettes separating the inner and outer cusps. All of the molars are characterized by strong parastyles and mesostyles. The metastyle is weaker than the parastyle on M^1 and M^2, but on M^3 it is as prominent as the parastyle. Strong vertical ribs mark the buccal surfaces of both the paracone and metacone. These ribs are relatively stronger in *M. agatensis* than in *P. heterodontus.* But, as in the latter, the protocones on all the molars are anteroposteriorly narrower than the hypocones. M^2 is similar to M^1, but larger. In the type (A.M.N.H. No. 14255) M^2 is the largest of the series, but in a more worn specimen (A.M.N.H. No. 14261) M^3 is the largest. M^3 differs from M^2 in having (1) the posterior lobe narrower than the anterior and (2) a stronger metastyle. In *M. agatensis* the anteroposterior length of the posterior lobe of M^3 is about the same as the anterior lobe, but in *P. heterodontus* the posterior lobe is more anteroposteriorly expanded.

Lower Dentition: I_3, C, P_4, M_3. The lower dentition is completely represented in the type (A.M.N.H. No. 14255), and except for I_1 is complete in referred mandible (A.M.N.H. No. 14259). The lower incisors are large and crowded, with each incisor overlapping the preceding one.

Both I_1 and I_2 are spatulate and procumbent; I_1 is slightly expanded and I_2 greatly expanded toward the occlusal surface. I_3 differs from the preceding incisors in being less spatulate and more erect. A short space separates the I_3 and the laterally compressed and semi-incisiform canine. In *M. agatensis* the canine is less caniniform and more anteriorly situated than in *P. heterodontus.* A moderately long diastema separates the canine from a small, laterally compressed, and single-rooted P_1. In the type, P_1 is simple and almost peglike, consisting primarily of a low median cusp. The right side of the mandible has two almost identical P_1s that are situated so closely, one behind the other, that they are actually touching. In the referred mandible (A.M.N.H. No. 14259), the P_1 is anteroposteriorly longer and more premolariform with a low, median cusp that connects weak anterior and posterior cusps by narrow crests. Between P_1 and P_2 is a long diastema. P_2 is anteroposteriorly elongate, laterally compressed, and characterized by a low median protoconid, connected to a small anterior cusp (paraconid) and to an even smaller and less distinct posterior cusp (entoconid) by narrow crests. No distinct metaconid is present, but the lingual side of the protoconid is slightly enlarged and rounded at this point. P_2 in *M. agatensis* is more complex and proportionally larger than in *P. heterodontus.* In *M. agatensis,* P_3 is bladelike, anteroposteriorly elongate, and laterally compressed, and except for its larger size and more distinct cusps, it is similar to P_2. P_3 is characterized by a larger anterolingually flexed cusp (paraconid) and a large but rather low protoconid; posterior to the protoconid is a smaller lingually flexed cusp. P_4 is similar to P_3 except for a distinct entoconid and hypoconid that unite to enclose a small fossettid. In addition, the protoconid is situated more anteriorly with crests that lead posteriorly to the entoconid and hypoconid.

Except for shorter crowns, stronger metastylids, and smaller size, the lower molars of *M. agatensis* do not differ substantially from those of *Protolabis heterodontus.* In *M. agatensis* the stylids are reduced in comparison with those of the upper molars and only the metastylid is really strong. In both mandibles (A.M.N.H. Nos. 14255, 14259), M_1 is so worn that the presence of the parastylid and metastylid can only be surmised, but a small entostylid is present. A less worn M_2 has a weak parastylid and moderately strong metastylid and entostylid. Unlike *P. heterodontus,* the metastylid remains distinct nearly to the base of the tooth. The buccal surfaces of the metaconid and entoconid in *M. agatensis* are almost smooth, showing only a trace of a vertical rib. Both M_1 and M_2 narrow slightly toward the roots but M_3 tends to be anteroposteriorly longer. The third molar has three lobes, the last lobe being much smaller than the two

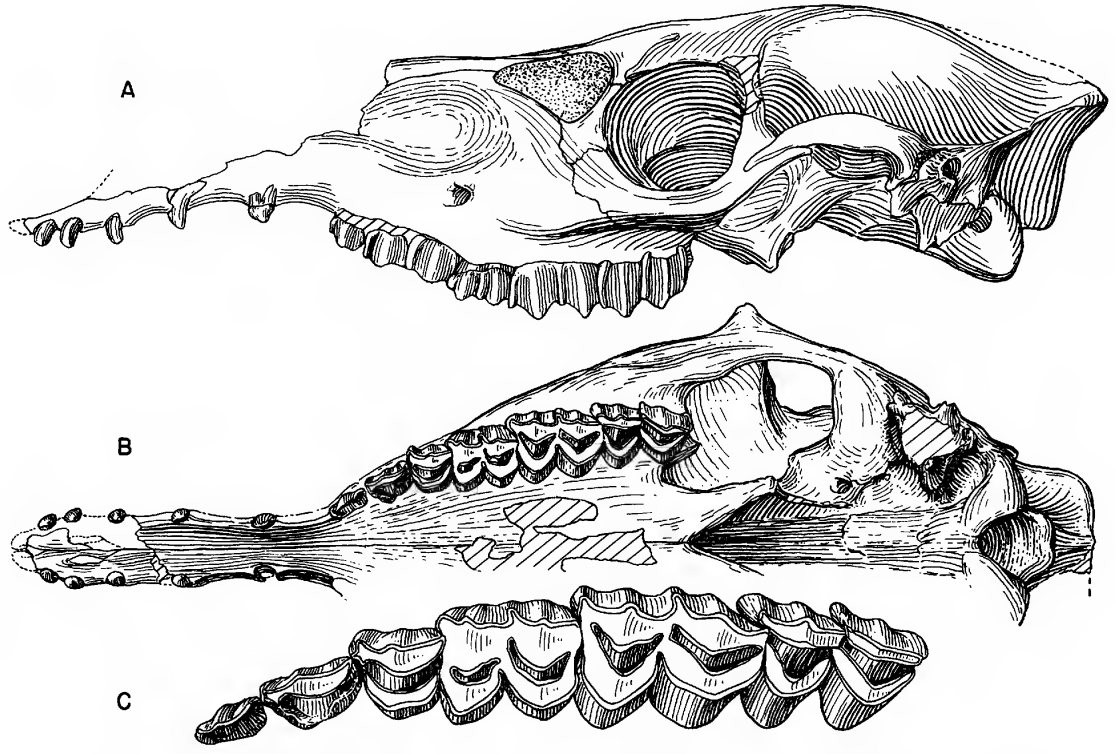

FIG. 1. *Michenia agatensis,* new genus, new species. Type, partial skeleton, A.M.N.H. No. 14255, from the Upper Harrison beds of Peterson, 1906 (=the Marsland Formation of Schultz, 1938), 6 miles northeast of the former post office of Agate, Sioux County, Nebraska. A. Lateral view. ×½. B. Palatal view. ×½. C. P^2–M^3, occlusal view. ×1. (See the mandibular ramus and limbs, figs. 2 and 3).

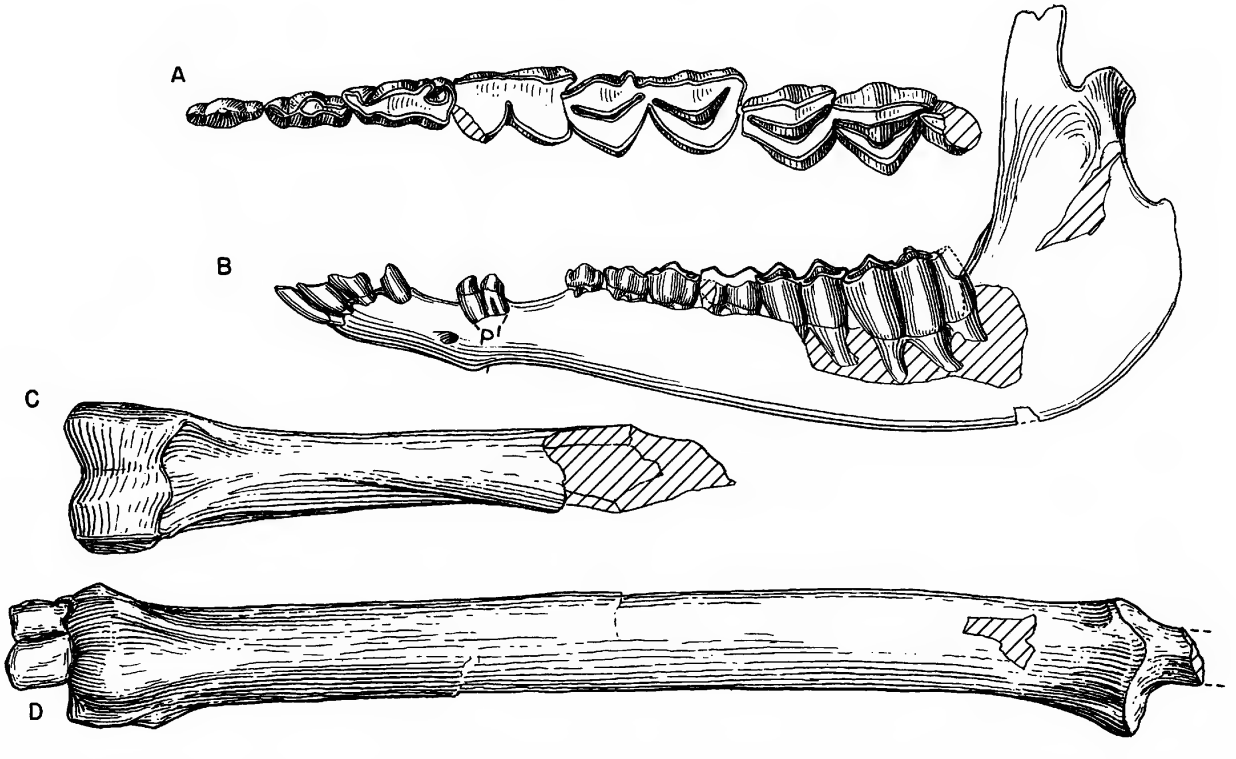

FIG. 2. *Michenia agatensis*. Type, partial skeleton, A.M.N.H. No. 14255, from the Upper Harrison beds of Peterson, 1906 (=the Marsland Formation of Schultz, 1938), 6 miles northeast of the former post office of Agate, Sioux County, Nebraska. A. Right P_2–M_3, occlusal view, reversed. ×1. B. Right mandibular ramus, lateral view, reversed. ×½. C. Left partial humerus, anterior view. ×½. D. Right radius, scaphoid, and lunar, anterior view, reversed. ×½. (See skull and rear limb, figs. 1 and 3 respectively).

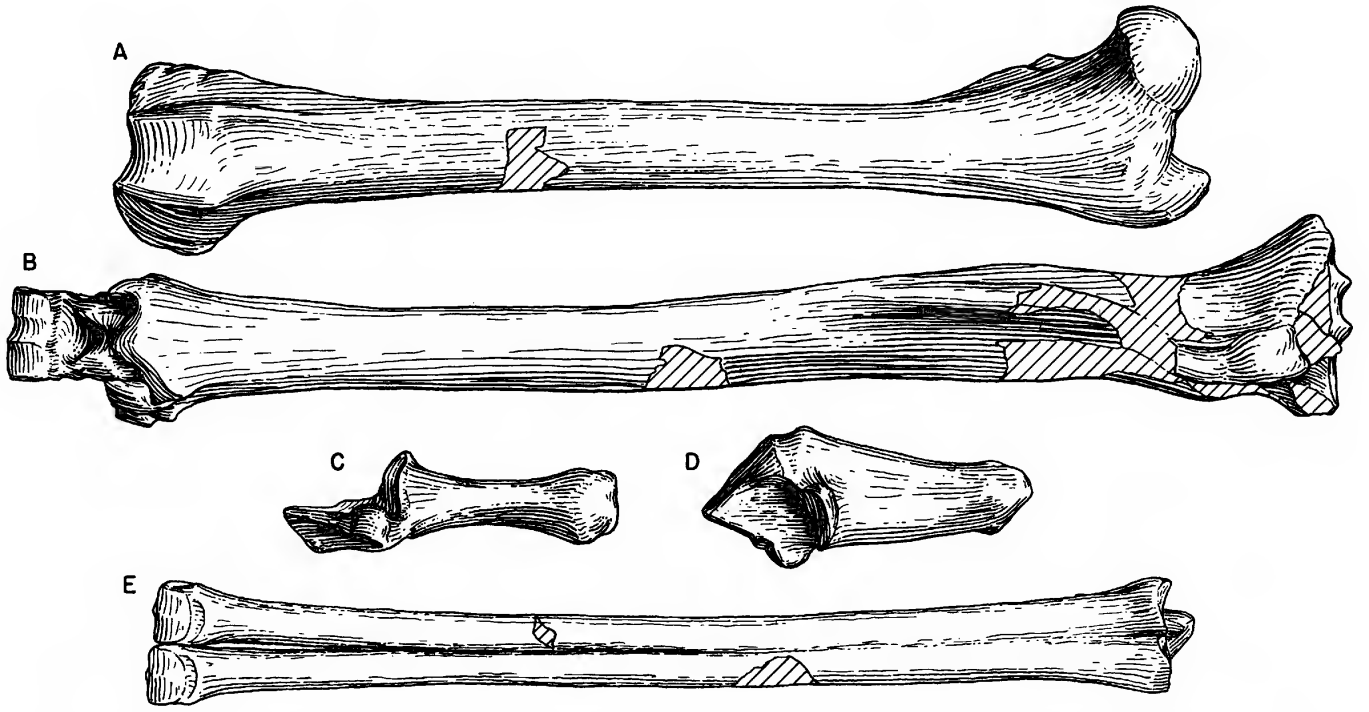

FIG. 3. *Michenia agatensis.* Type, partial skeleton, A.M.N.H. No. 14255, from the Upper Harrison beds of Peterson, 1906 (=the Marsland Formation of Schultz, 1938), 6 miles northeast of the former post office of Agate, Sioux County, Nebraska. A. Left femur, anterior view. B. Left tibia, malleolar, and astragalus, anterior view. C, D. Left calcaneum. C. Anterior view. D. Mesial view. E. Left metatarsus, anterior view. All ×½. (See skull, mandible and more limbs, figs. 1 and 2).

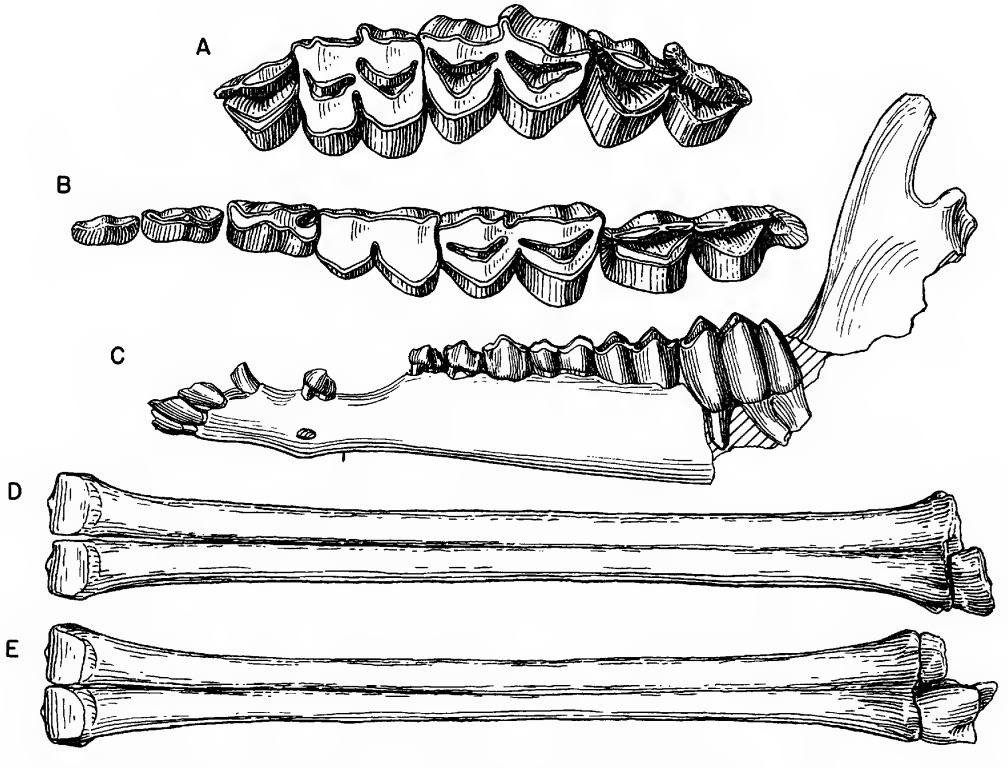

FIG. 4. *Michenia agatensis.* Referred partial skeleton, A.M.N.H. No. 14259, from the Upper Harrison beds of Peterson, 1906 (=the Marsland Formation of Schultz, 1938), 5 miles northeast of the former post office of Agate, Sioux County, Nebraska. A. Detached teeth, right P^4-M^3 (M^3 restored from left), occlusal view, reversed. ×1. B. Partial mandible, P_2-M_3 (M_3 reversed from the right), occlusal view. ×1. C. Lateral view (M_3 reversed from the right). ×½. D. Right metacarpus and unciform, anterior view, reversed. ×½. E. Right metatarsus, cuboid and ectocuneiform, anterior view, reversed. ×½.

preceding ones. Actual crown height of the unworn second lobe (A.M.N.H. No. 14259, fig. 4) is 21 mm., equivalent to about 75 per cent of the length of M_3 and less than in the later occurring *P. heterodontus.* M_3 is characterized by a faint parastylid, a strong metastylid, and a weak entostylid, and as in M_2, the metaconid and entoconid have only a trace of a vertical rib. The hypoconulid is narrow at the top but broadens anteroposteriorly toward the root and is proportionally smaller than in *P. heterodontus.*

MANDIBLE: The horizontal ramus is long, shallow, and gradually narrows anteriorly. The mandible of the type of *M. agatensis* reflects the same specialization as in the skull, i.e. a long slender muzzle. As in *P. heterodontus,* the symphysis is fused and is long, narrow, and deeply hollowed lingually, extending posteriorly to directly beneath P_1. The diastemata between the canine, P_1, and P_2, are pinched to a sharp ridge. Apparently the position of the mental foramen is variable; it is anterior to P_1 in the type (A.M.N.H. No. 14255, fig. 2) and beneath P_1 in the referred mandible (A.M.N.H. No. 14259, fig. 4). A rounded angle of the mandible continues upward to the strong posterior hooklike projection so typical of the camelids. The condyle of the mandible is wide transversely and the articular surface slopes mesially and downward. Although the coronoid process is incomplete, enough remains to show that it is very thin, delicate, and slopes in a slightly posteromesial direction. Both the symphysis and the horizontal ramus in *M. agatensis* are shallower than in *P. heterodontus.* In the latter, the symphysis is noticeably deep near the posterior border, deep enough to change the entire ventral profile of the mandible.

LIMBS: Two partial skulls and the dentition of a third individual of *M. agatensis* have associated limbs; all limb elements are represented. Other than the morphological differences observed here in the metapodials, the limbs of *M. agatensis* are similar to those of *P. heterodontus,* except in size and proportion; therefore, no detailed description is given. As indicated by the associated limbs of *M. agatensis,* the ratio of metapodial length to the other limbs and to the length of the skull is significantly different from that of *Protolabis.*

The metapodials in *M. agatensis* are proportionally longer, more slender, and less solidly fused than in *P. heterodontus.* Characters that indicate the metapodials of *M. agatensis* are less advanced than those of *P. heterodontus* are: (1) a deeper groove along the line of fusion in both the metacarpus and the metatarsus and (2) a greater proximal extension of the anterodistal separation of the distal ends of the metacarpus and the metatarsus.

GENERIC LIMB PROPORTIONS: Because of inadequate associated skeletal remains of *Protolabis heterodontus,* the limb proportions of *Michenia agatensis* are compared with those of a partial skeleton (F:A.M. No. 38711) of an

undescribed species of *Protolabis* of late Hemingfordian age from the Nambé area in New Mexico. The length of the metacarpus in *Michenia* slightly exceeds that of the metatarsus (A.M.N.H. No. 14259, table 3), whereas in the *Protolabis* skeleton (F:A.M. No. 38711) the metacarpus is slightly shorter than the metatarsus. Moreover, the length of the metacarpus apparently exceeds the basal length of the skull and is proportionally longer than in *Protolabis*. This deduction is based upon the measurements of the associated remains of the type (A.M.N.H. No. 14255, table 3) in which the length of the metatarsus, which is less than that of

TABLE 3

MEASUREMENTS (IN MILLIMETERS) OF LENGTH OF LIMBS OF *Michenia agatensis*, NEW SPECIES

	A.M.N.H. No. 14255[a]	A.M.N.H. No. 14259	A.M.N.H. No. 14261
Humerus	—	—	—
Radius	270.0	—	285.0
Metacarpus	—	230.0	271.0
Femur	271.0	(242)[b]	—
Tibia	(307)	267.0	—
Metatarsus	257.0	220.0	—

[a] Type of *Michenia agatensis*, new species.

[b] Measurements enclosed in parentheses are approximate.

the metacarpus (A.M.N.H. No. 14259, table 3), is 257 mm. and the basal length of the skull is only 237 mm. The metacarpus is also proportionally longer relative to the radius than in *Protolabis*. In *M. agatensis* (A.M.N.H. No. 14261) the length of the metacarpus (271 mm.) is only about 5 per cent less than that of the radius (285 mm.). In the *Protolabis* skeleton (F:A.M. No. 38711) the metacarpus-metatarsus proportion is reversed from that of *Michenia* with the length of the metacarpus (265 mm.) slightly less than that of the metatarsus (267 mm.). Also, in contrast to *Michenia*, the length of the metacarpus (265 mm.) in the *Protolabis* skeleton is much less than the basal length (330 mm.) of the skull and proportionally shorter relative to the length of the radius (308 mm.). In later occurring species of *Protolabis* the metapodials are proportionally shorter than those of the *Protolabis* skeleton (F:A.M. No. 38711) and the length of the metacarpus is always less than that of the metatarsus.

SUMMARY

Since *Protolabis* Cope (1876) was described, species of this genus, in-

cluding the type species have frequently been confused with those of *Procamelus* and *Miolabis.* A brief taxonomic history of *Protolabis,* as well as a clarification of the type species, is given along with characters that distinguish *Protolabis* from both *Procamelus* and *Miolabis. Michenia agatensis,* a specialized camelid of smaller size, near the base of the evolutionary radiation of the protolabines, is also described. Although its ancestry is unknown, *Michenia agatensis* more closely resembles *Dyseotylopus migrans* Stock from the upper part of the Sespe Formation of California than any other known Arikareean camelid.

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